

PARTHENOGENETIC REPRODUCTION AND ITS INHERITANCE  
IN SCHIZAPHIS GRAMINUM (RONDANI)

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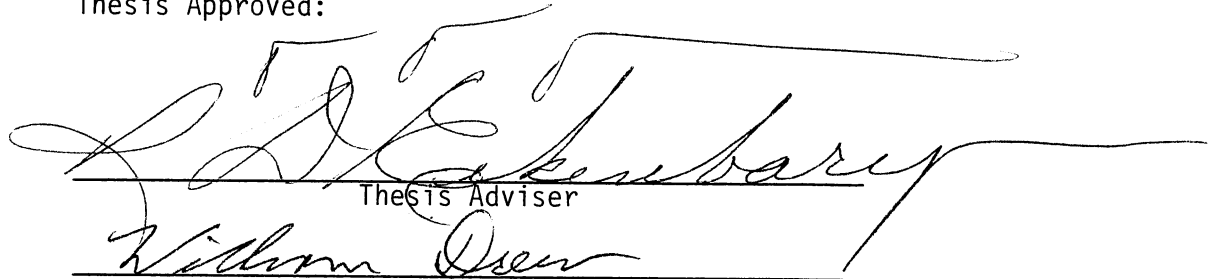
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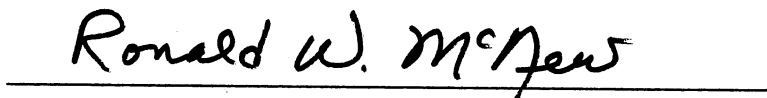



PARTHENOGENETIC REPRODUCTION AND ITS INHERITANCE  
IN SCHIZAPHIS GRAMINUM (RONDANI)

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## PREFACE

Trained manpower is one of the major constraints in the development of third World countries. It is with this understanding that international organizations such as the United Nations are involved in training students from these countries in different fields including agriculture. It is this effort by international organizations and governments that have led to my training in the United States of America for my master's degree in entomology.

Many people have been helpful and I wish to express my sincere gratitude to the following: Dr. R. D. Eikenbary, my major adviser, who effectively guided me through my classwork and research work. Dr. R. W. McNew and Dr. W. A. Drew who served in my graduate committee, for their constructive assistance in correcting this thesis. In addition Dr. R. W. McNew for his initial guidance, his help in analyzing the data and interpreting the results. Mr. K. Dorschner and Mr. L. C. Sumner for their technical assistance.

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## CHAPTER I

### INTRODUCTION

Normally greenbug, Schizaphis graminum (Rondani), found in the field are alate or apterous females reproducing parthenogenetically and ovoviparously. Sexual forms of this aphid do occur in the field, but in the U.S., eggs from mated sexuals have not been demonstrated to be viable (Mayo and Starks 1972). Therefore, greenbug population growth in the field is attributed to parthenogenetic reproduction.

Greenbug reproduction studies in regard to prereproductive period, reproductive period, postreproductive period, longevity, fecundity and offspring per day of reproductive life include that of Hunter (1909), Webster and Philips (1912), Wadley (1931), and Daniels (1963, 1967). With mean monthly temperature ranging from 70°F to 80°F, Glenn (1909) reported an average longevity of 35.2 days, a reproductive period of 22.7 days and fecundity of 55.4 offspring. At a constant temperature of 80° F results of Headlee (1914) showed that 6 days elapsed before greenbugs started reproducing. They lived for an average of 12 days and produced an average of 3.1 offspring per day of reproductive life. In a similar study, at an average temperature of 79°F greenbug reproduced 69.3 offspring within a mean of 19.3 days of reproductive life and lived for 20.3 days. The average number of offspring produced per day were 3.58 (Wadley 1936). Different results over experiments is suggested to be due to using different host material and insect strain (Wood and Starks



1972).

Although the ultimate goal was not to determine heritability, studies which attempted to look at how these reproductive variables of greenbug vary from parent to offspring were carried out by Luginbill and Beyer (1918) and Tucker (1918).

As in most other characteristics, observed variation (phenotypic variation) in reproductive variables of a parthenogenetic greenbug is the result of genotypic and environmental variation. Heritability is a measure of the proportion of phenotypic variance attributable to the variation of genotypes which is the genotypic variance. This variance can be estimated from the resemblance of relatives.

Most literature related to inheritance of variation in parthenogenesis is intraclonal and conflicting. Warren (1899, 1901) reported the occurrence of inherited variation within clones of a daphnia and an aphid species. Cognetti (1961, 1962), Pagliai (1967), Orlando (1965) interpreted their results from studies made on various parthenogenetic aphids as demonstrating genetic recombination. Mitotic recombination as the possible cause of enzyme variation and therefore the occurrence of some kind of genetic recombination is reported by Beranek and Berry (1974).

On the other hand, a parthenogenetic female of Daphnia magna (Straus) heterozygous for an enzyme variant produced offspring that were only heterozygous indicating the absence of recombination (Hebert and Ward 1972). Sexual crosses of known phenotypes made in this same species resulted in progenies having observed proportions very close to the expected phenotypic ratios. Correlation between parent and offspring for length of the body along their longest line in two species of

cladocera was found to be nonsignificant while a partial inheritance for distance between eyes and length of antenna was observed in Macrosiphum antherinii (Macch) (Agar 1914). Similarly correlation for tentacle variation in hydra was not significant (Lashley 1915). Ewing (1916) reared Aphis avenae (Fabricius) continuously for 87 generations in which his attempt to shift the mean values of 3rd and 4th antennal segment by selection was unsuccessful.

After a detailed study of alate morph production and inheritance of esterase variants in Myzus persicae (Sulzer) and caudal hair alteration index in Acyrtosiphon pisum (Harris), Blackman (1979) reported that there is a general genetic stability in these parthenogenetically reproducing aphids and concluded that it is not the general rule to observe genetic recombination and considered parthenogenesis in aphids as ameiotic or apomictic. He further explained how mutation, mitotic recombination, variability of gene expression and contamination of laboratory clones could give rise to the intraclonal variations reported in the literature.

Although literature in which genetic variation, expressed in terms of heritability, in populations of parthenogenetic aphids is lacking, many workers including Georghiou (1963), Sudderuddin (1973), Eastop and Bank (1970) and Needham and Sawicki (1971) have indicated the existence of variation. In Greenbug, several biotypes identified in the past few years (Wood 1961, Harvey and Hackerott 1969) is a good indication that genetic variation exists.

It is, therefore, the objective of this experiment to determine the degree of genetic control in parthenogenetic reproduction of the greenbug.

## CHAPTER II

### METHODS AND MATERIALS

Greenbugs were collected from ten localities (Chickasha, Hobart, Kingfisher, Perkins, Ponca City, Roosevelt, Sparks, Wichita, Yale, Stillwater) within Oklahoma in April and May 1982. One adult greenbug from each collection was cultured separately in an environmental chamber maintained at a temperature of 23°C and 16 hours of daylight respectively. Sexual forms of greenbug appear when temperature and daylight is reduced below 21°C and 12 hours of light respectively (Wadley 1931). Therefore, the condition in the chamber assures that only parthenogenetic reproduction occurs without the appearance of the sexual forms.

Three seeds of Triumph 64 wheat were placed in a 7.6cm diameter plastic pot containing a 3:1:1 mixture of soil, sand and peat. Three days after germination all, but one plant, were removed from the pot. One week after germination ten adult greenbugs, one from each of the ten localities were released on ten potted plants covered with plastic cages with clothcovered ventilation holes. After 24 hours the adult and all but one offspring were removed from each of the ten potted plants. The remaining nymph was left to grow and when reproduction began, daily counts of offspring were made until the adults were dead. Furthermore, the first (type 1) and two other offspring (type 2 and 3) born at one week intervals were each kept in a similar one plant pot and placed in the same chamber. When they started reproducing, daily offspring counts

were made and recorded in a similar manner to their mothers. All pots were assigned at random in the chamber. Plants were changed as needed (usually once a week) and the whole procedure was replicated three times for each locality except Kingfisher which was replicated four times.

Heritability estimates were calculated by regression of offspring on parent.

## CHAPTER III

### RESULTS AND DISCUSSION

Daily offspring counts by type and location are shown in Table I (Appendix). Missing counts of type 1, type 2 or type 3 was due to (1) early death, at prereproductive or early reproductive period, of the insect, and the (2) adult mother stopping reproduction before giving birth to type 2 or type 3.

The smallest number of offspring produced by one greenbug in one day is 0 and the largest 11 (Table I, Appendix) while offspring per day of reproductive period ranges from 2.0 to 7.1; reproductive period from 4 to 26; prereproductive period from 5 to 11; postreproductive period from 0 to 27; longevity from 18 to 50 and fecundity from 8 to 109 (Table II, Appendix). There are 97 of 110 observations having a prereproductive period of either 5 or 6 days, 10 with 7 days, 2 with 8 days and one with 11 days. Towards the end of the reproductive period, generally, reproduction starts to decline and in some cases the greenbug may skip one or two days in between without giving birth to a single offspring.

The mean values of each reproductive variable calculated by type and by location are shown on Tables III and IV, respectively. No significant difference was observed within reproductive variables due to location while significant differences were observed due to types for postreproductive period and longevity. There are 13 observations where the postreproductive period lies between 0 and 5 days, out of which 8

TABLE III  
 MEAN VALUES OF REPRODUCTIVE VARIABLES BY TYPE OF A PARTHENOGENETICALLY  
 REPRODUCING SCHIZAPHIS GRAMINUM (RONDANI).  
 STILLWATER, OK, SUMMER 1982

Reproductive Variables <sup>a</sup>	Mean Values			
	Type <sup>b</sup>			
	P	1	2	3
PP	5.8	6.1	5.7	6.0
RP	17.7	17.7	16.9	17.0
PORP	14.9	16.4	19.0	19.2*
LONG	38.4	40.9	41.9	42.2*
FECU	78.6	84.2	81.7	83.5
OPRP	4.5	4.8	4.8	5.1

<sup>a</sup>Reproductive variables are: PP = prereproductive period; RP = reproductive period; PORP = post-reproductive period; LONG = longevity; FECU = fecundity; OPRP = offspring per day of reproductive period.

<sup>b</sup>Typea are: P = parent; 1 = first offspring; 2 = offspring one week after larviposition; 3 = offspring two weeks after larviposition.

TABLE IV  
 MEAN VALUES OF REPRODUCTIVE VARIABLES BY LOCATION OF A  
 PARTHENOGENETICALLY REPRODUCING SCHRIZAPHIS  
GRAMINUM (RONDANI) STILLWATER, OK.  
 SUMMER 1982

Reproductive Variables <sup>a</sup>	Mean Values									
	Locations <sup>b</sup>									
	A	B	C	D	E	F	G	H	I	J
PP	6.1	6.2	5.8	5.9	5.8	5.9	5.6	5.9	6.1	5.8
RP	17.5	14.5	17.5	19.7	18.2	17.3	16.6	18.4	16.1	16.3
PORP	17.5	9.2	18.5	14.8	18.4	16.4	20.0	16.9	18.0	19.0
LONG	41.6	29.8	41.9	40.3	42.3	40.3	43.2	41.2	39.7	41.5
FECU	76.1	64.3	81.8	90.3	90.3	84.2	81.0	84.8	76.2	82.3
OPRP	4.5	4.1	4.8	5.0	5.0	5.0	4.9	4.7	4.7	5.1

<sup>a</sup>Reproductive variables are: PP = prereproductive period; RP = reproductive period; PORP = postreproductive period; LONG = longevity; FECU = fecundity; OPRP = offspring per day of reproductive period.

<sup>b</sup>Locations are: A = Kingfisher; B = Wichita; C = Hobart; D = Sparks; E = Chickasha; F = Roosevelt; G = Stillwater; H = Perkins; I = Yale; J = Ponca City

are for parents (type P). This lowered the average postreproductive period for parent to 14.9 as compared to 16.4, 19.0 and 19.2 (Table III) for type 1, 2 and 3, respectively, and, in turn, gave rise to a lower average longevity for parents. Location B (Wichita) has the lowest average for most reproductive variables (Table IV). This is partly because there was one greenbug that produced only 8 offspring in four days of reproductive period.

Mean values of reproductive variables calculated over type and location are: prereproductive period, 5.9; reproductive period, 17.3; postreproductive period, 17.2; longevity 40.7; fecundity 81.9; and offspring per day of reproductive period 4.8. This result, in general, agrees with that of Daniels (1957, 1963, 1967) and Muddathir (1976). Different results have been obtained in separate experiments carried out under similar temperature ranges. These differences could arise from the use of different biotypes or hosts (Wood and Starks 1972).

The objective of this experiment is to determine the degree of genetic control in parthenogenetic reproduction of the greenbug. Table V shows heritability estimates (regression of offspring on parent) of the six reproductive variables by type and pooled over type and their corresponding standard errors. All pooled heritability estimates except offspring per day of reproductive period are not significant. Type 3 offspring has a higher heritability estimate than type 1 and 2 but no significant difference was observed except for longevity. Offspring per day of reproductive period has the highest and significant estimate ( $0.23 \pm 0.11$ ) while longevity the lowest ( $0.02 \pm 0.09$ ). Longevity is the sum of the prereproductive, reproductive and postreproductive periods which all are characterized by variation. The variation of the sum of



TABLE V  
HERITABILITY ESTIMATES AND STANDARD ERRORS BY TYPE AND POOLED OVER  
TYPE FOR REPRODUCTIVE VARIABLES OF A PARTHENOGENETICALLY  
REPRODUCING SCHIZAPHIS GRAMINUM (RONDANI)

Reproductive variables <sup>a</sup>	Heritability Estimates ± S.D.			Heritability Estimates
	Type <sup>b</sup>			Pooled Over Type ± S.I.
	1	2	3	
PP	-0.26 ± 0.19	-0.18 ± 0.28	-0.52 ± 0.62	-0.31 ± 0.21
RP	0.03 ± 0.16	0.01 ± 0.16	0.18 ± 0.23	0.04 ± 0.10
PORP	-0.03 ± 0.16	-0.02 ± 0.13	0.36 ± 0.16	0.10 ± 0.09
LONG	0.01 ± 0.17	-0.17 ± 0.14	0.37 ± 0.15	0.02 ± 0.09
FECU	0.03 ± 0.18	0.13 ± 0.24	0.47 ± 0.26	0.12 ± 0.12
OPRO	0.09 ± 0.12	0.33 ± 0.20	0.37 ± 0.29	0.23 ± 0.11

<sup>a</sup>Reproductive variables are: PP = prereproductive period; RP = reproductive period; PORP = postreproductive period; LONG = longevity; FECU = fecundity; OPRP = offspring per day of reproductive period.

<sup>b</sup>Types are: 1 = first offspring; 2 = offspring one week after larviposition; 3 = offspring two weeks after larviposition.

these three reproductive variables which make up longevity is equal to the sum of their individual variation plus the covariances among themselves. This additional variation may have contributed to the lower heritability.

Heritability estimates calculated by regression of offspring on parent, discussed above, can also be expressed graphically. This is illustrated on Figures 1 to 6 for each reproductive variable. Each point on the graph represents the value of individual mother (measured along the horizontal axis), and the mean value of the offspring of each mother (measured along the vertical axis). The axes intersect at the mean value of all parents and all offspring. The linear regression of offspring on parent is represented by each sloping line whose slope estimates heritability. The graph reflects more or less the same heritability estimates in Table V. For example the sloping line for longevity is almost a horizontal line indicating the smallness of heritability which would have been zero if the line is parallel to the horizontal axis. Increase in the slope of line, which can happen when the similarity between parent and offspring increases, means increase in heritability.

As indicated above, no genetic variation, in general, was observed in the population of greenbug collected from different localities. But many workers have shown the existence of variation within population of parthenogenetic aphids. Georghiou (1963) and Sudderuddin (1973) in green peach aphid, Eastop and Bank (1970) in peach potato aphid and, Needham and Sawicki (1971) in Myzus persicae observed different individual reaction to insecticides within a species. Variable esterase enzyme pattern, as a result of genetic difference was observed among different clones of Aphis fabae and Myzus persicae derived from field and

Figure 1. Regression of offspring on parent for prereproductive period  
in a parthenogenetically reproducing Schizaphis graminum  
(Rondani). Stillwater, OK, 1982.

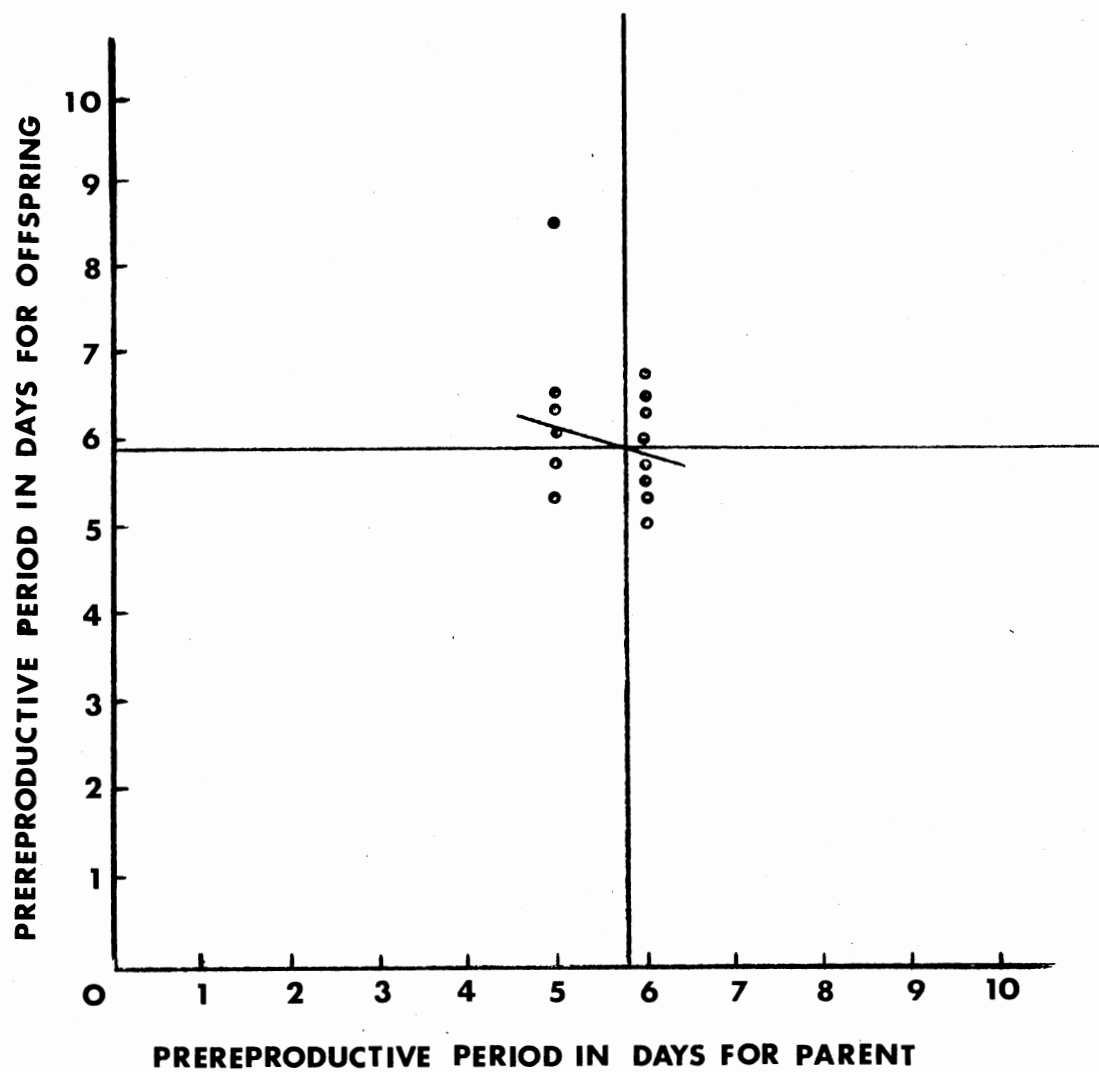


Figure 2. Regression of offspring on parent for reproductive period in a parthenogenetically reproducting schizaphis graminum (Rondani). Stillwater, OK, 1982.

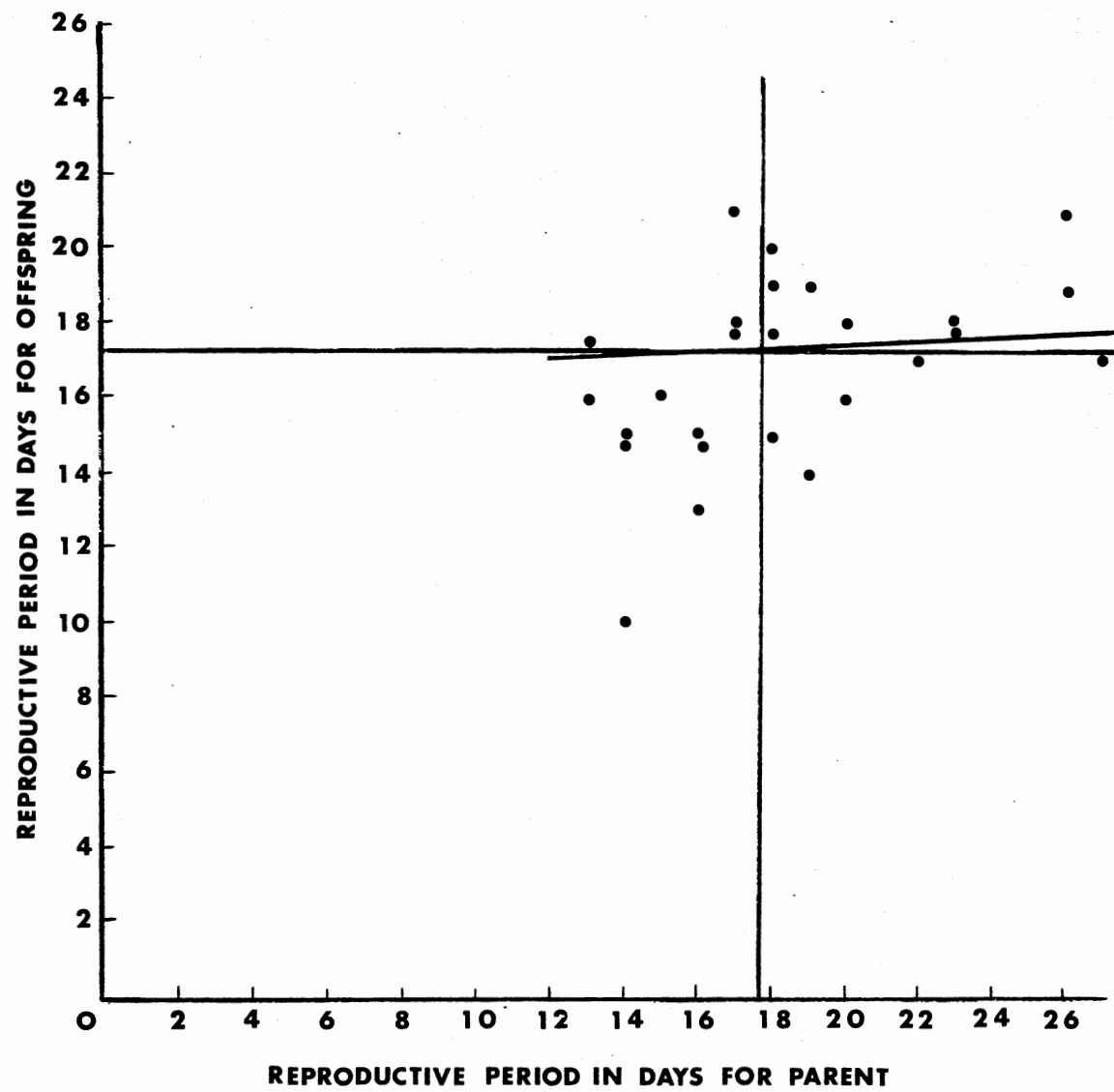
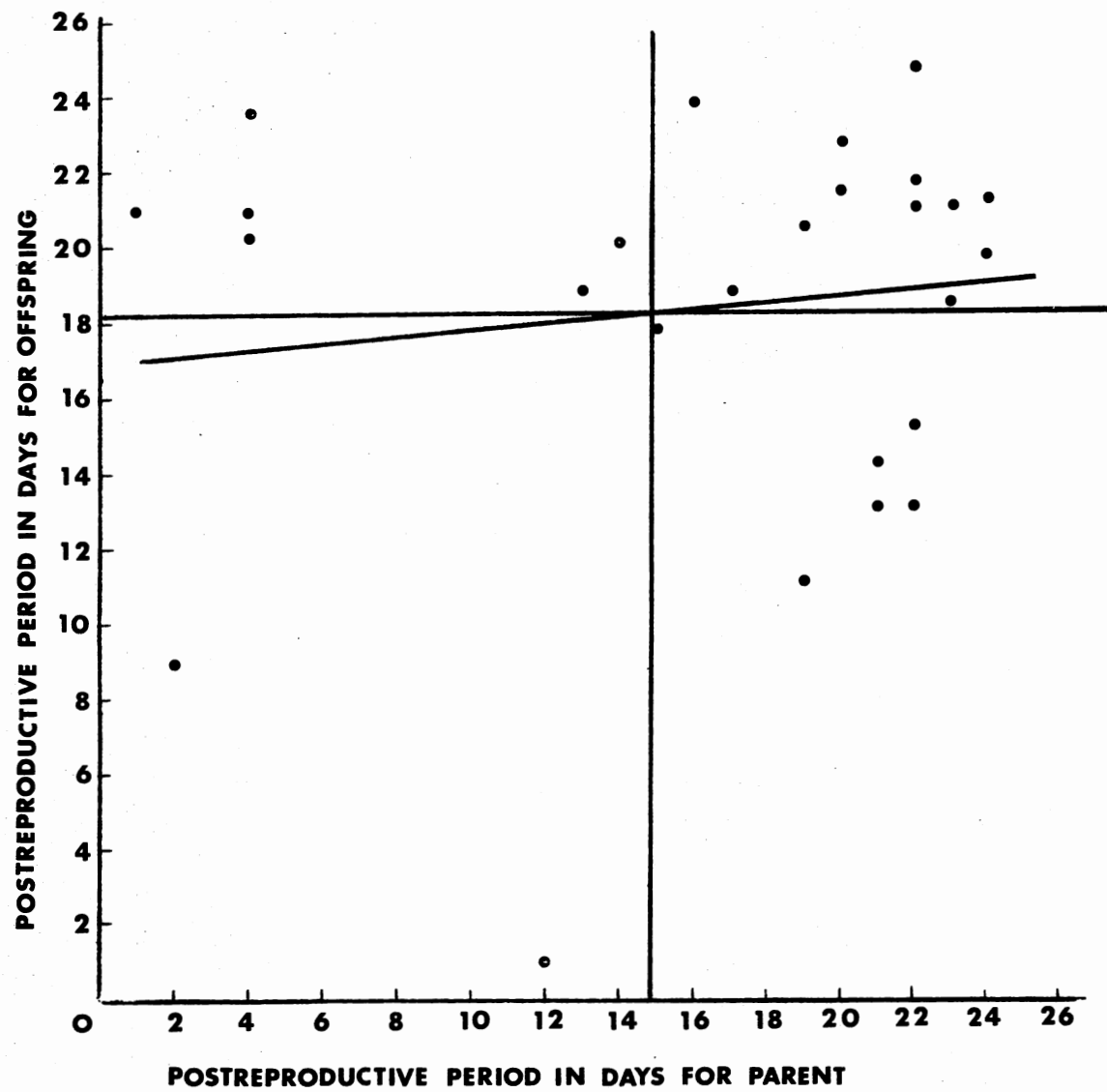


Figure 3. Regression of offspring on parent for postreproductive period  
in a parthenogenetically reproducing Schizaphis graminum  
(Rondani). Stillwater, OK, 1982.





glasshouse population (Beranek 1974).

Regarding genetic variation in greenbug, several biotypes have been discovered in the past two decades including the B biotype identified in a greenhouse here in Stillwater (Wood 1961) and the C biotype by Harvey and Hackerott (1969). Genetic segregation as a result of sexual generation is one possible source of variation and, therefore, the development of biotypes. Despite the fact that oviposition by greenbug was observed in greenhouse studies in Texas and Oklahoma (Daniels 1956, Wood et al. 1969) and in the field by Webster and Philips (1912), eggs from mated sexuals have not been demonstrated to be viable. But, on the other hand, the potential of ova of sexuals of greenbug to develop, if placed under proper environmental conditions, was demonstrated by Mayo and Starks (1972).

Intraclonal difference could also contribute to variation in populations of aphids. Parthenogenetic clones are generally considered to stay genetically stable because of no segregation and, therefore, contribute very little to genetic variation (Blackman 1979). But it is important to note that there are some intraclonal variations observed (Beranek and Berry 1974, Orlando 1965, Pagliani 1967) which Blackman (1979) considers might be due to mitotic segregation, mutation or variability of gene expression.

Therefore, it is reasonable to expect some kind of genetic variation in regard to the reproductive variables in the population of greenbug collected from ten different localities. It has been possible, at least, to detect heritable variation in one of the six reproductive variables (offspring per day of reproductive period) since a significant heritability estimate ( $0.23 \pm 0.11$ ) was obtained. But why was it not

Figure 4. Regression of offspring on parent for longevity in a parthenogenetically reproducing Schizaphis graminum (Rondani). Stillwater, OK, 1982.

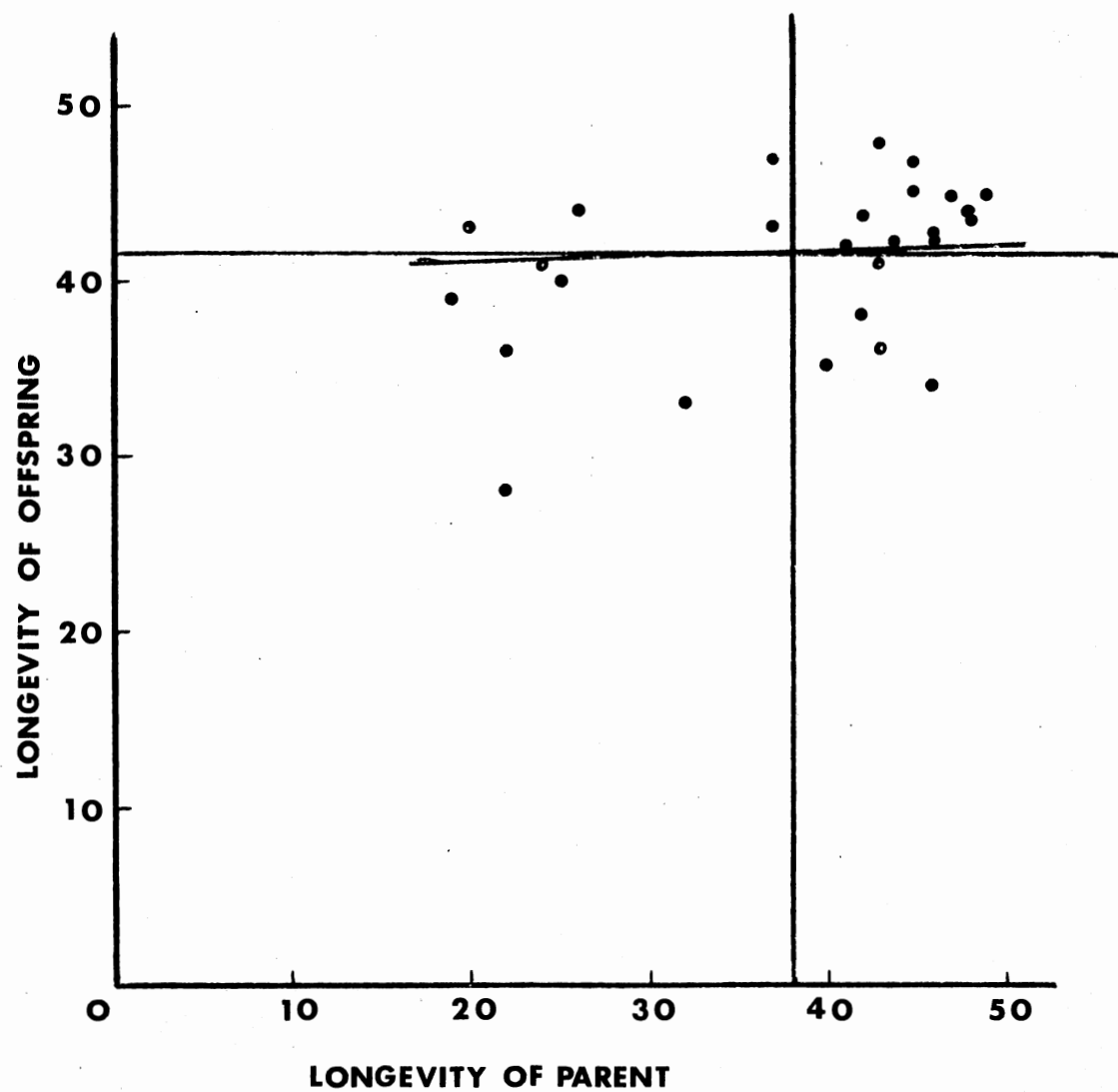


Figure 5. Regression of offspring on parent for fecundity in a parthenogenetically reproducing Schizaphis graminum (Rondani). Stillwater, OK, 1982.

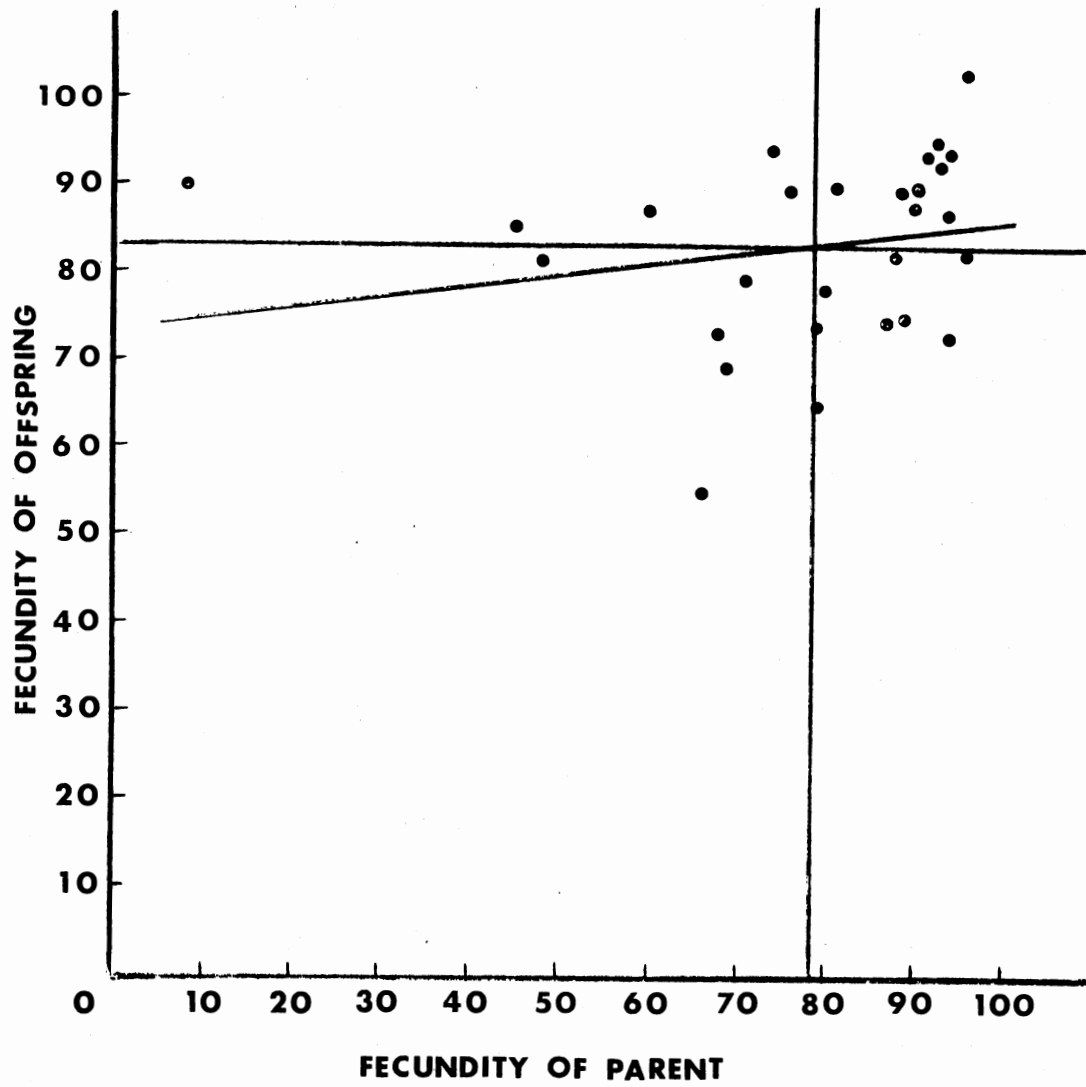
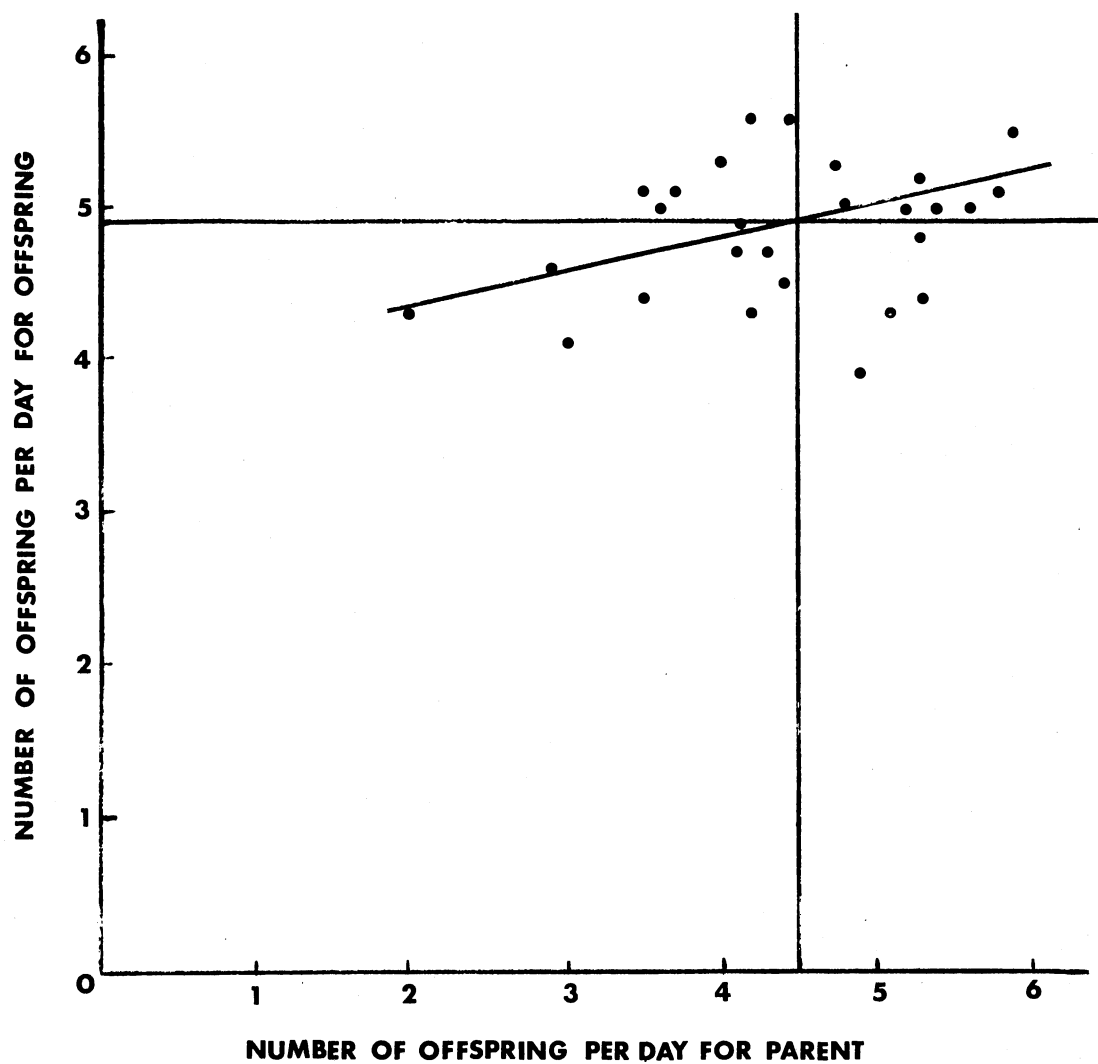


Figure 6. Regression of offspring on parent for offspring perday of reproductive period in a parthenogenetically reproducing Schizaphis graminum (Rondani). Stillwater, OK, 1982.



possible to observe variation in general?

Because of lack of the chromosome condensation phase in the first oocyte in Acyrtosiphon pisum (Blackman 1978) only progenies born after the first week of larviposition were included in a selection experiment (Blackman 1979). These progenies born from oocytes that have not gone through the chromosome condensation phase were considered atypical. It is not really clear how much the similarity or difference between parent and offspring changes because of this mode of oocyte development. Types 1 and 2 occurred during the first week of larviposition while type 3 occurred later. The higher heritability estimate of type 3 may be due to this mode of oocyte development. Therefore, the pooled estimate might have been larger if all three offspring (type 1, 2 and 3) were taken after one week of larviposition.

The other possible explanation for not observing genetic variation may be related to the fact that the nature of the character for which heritability is determined is connected to the magnitude of heritability. This was demonstrated in Drosophila melanogaster where heritability estimate for abdominal bristle number was 0.5 (Clayton et al. 1957) while thorax length, ovary size and egg production had 0.4, 0.3 and 0.2 respectively (Robertson 1957). This clearly shows that characters with low heritabilities are those connected with reproductive fitness. Therefore, low heritability is expected for the reproductive variables dealt in this experiment since they are related to reproductive fitness. It seems that we were not able to detect whatever variation exists due to its smallness.



## CHAPTER IV

### SUMMARY

This investigation carried out in a growth chamber was designed to determine the degree of genetic control of the different reproductive variables of a parthenogenetically reproducing greenbug, Schizaphis graminum (Rondani).

Greenbug sampels were collected from ten different localities within Oklahoma and each sample, represented by a single aphid, was raised separately in a growth chamber maintained at a temperature of 23°C and 16 hours of daylight which allows only parthenogenetic reproduction to occur.

Greenbug had an average prereproductive period of 5.9 days, a reproductive period of 17.3 days, postreproductive period of 17.2 days, longevity of 40.7 days, fecundity of 81.9 offspring and 4.8 offspring per day of reproductive period.

Heritability estimates were made by the regression of offspring on parent. The estimates are  $-0.31 \pm 0.21$  for prereproductive period;  $0.23 \pm 0.11$  for offspring per day of reproductive period;  $0.12 \pm 0.10$  for reproductive period and  $0.02 \pm 0.09$  for longevity. All except offspring per day of reproductive period are not significant. Evidence, at least, indicates that heritability of these reproductive variables is not large.

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TABLE I

DAILY OFFSPRING COUNT BY TYPE AND LOCATION INCLUDING THE PREREPRODUCTIVE PERIOD, OF A PARTHENOGENETICALLY REPRODUCING SCHIZAPHIS GRAMINUM (RONDANI), STILLWATER, OK. SUMMER 1982

				Daily Offspring Count																															
				Days																															
a	b	c	d	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
0	L	T	R																																
1	A	P	3	0	0	0	0	0	0	6	8	4	8	4	3	3	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	A	1	3	0	0	0	0	0	4	8	6	7	4	6	3	3	7	4	6	3	5	4	2	6	1	4	2	2	4	3	2	1	1	2	.
3	A	2	3	0	0	0	0	0	1	3	2	4	4	3	5	5	5	4	4	5	3	3	5	1	4	2	3	1	2	1	1	.	.	.	.
4	B	P	3	0	0	0	0	0	0	3	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5	B	1	3	0	0	0	0	0	0	3	8	6	6	9	5	6	7	3	3	5	6	5	2	5	3	1	3	1	2	1	.	.	.	.	
6	C	P	3	0	0	0	0	0	2	10	7	5	5	5	5	5	7	7	6	5	4	3	5	2	.	.	.	.	.	.	.	.	.	.	
7	C	1	3	0	0	0	0	0	9	9	8	11	8	6	6	3	2	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
8	C	2	3	0	0	0	0	0	2	7	8	6	7	5	4	3	5	6	5	4	7	2	5	2	2	2	0	1	.	.	.	.	.	.	
9	C	3	3	0	0	0	0	0	3	8	7	8	9	7	6	6	4	8	5	2	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.
10	D	P	3	0	0	0	0	0	2	6	10	8	8	9	5	8	8	4	6	5	5	5	3	2	2	.	.	.	.	.	.	.	.	.	
11	D	1	3	0	0	0	0	0	0	8	9	10	9	8	5	6	6	6	7	6	4	5	5	3	3	2	3	1	1	.	.	.	.	.	
12	D	2	3	0	0	0	0	0	6	8	8	9	7	7	9	6	4	7	4	6	7	6	2	1	1	.	.	.	.	.	.	.	.	.	
13	D	3	3	0	0	0	0	0	0	4	5	6	7	8	7	7	7	3	7	2	5	5	5	3	6	4	5	0	3	2	0	1	1	0	1
14	E	P	3	0	0	0	0	0	2	8	7	5	6	4	6	3	7	8	5	5	5	3	3	4	2	6	2	0	1	1	1	.	.	.	
15	E	1	3	0	0	0	0	0	0	8	6	5	7	5	3	4	3	8	6	8	8	5	4	2	4	4	4	1	1	.	.	.	.	.	
16	E	2	3	0	0	0	0	0	6	8	9	7	9	8	9	4	4	6	1	4	4	1	3	1	1	.	.	.	.	.	.	.	.	.	
17	E	3	3	0	0	0	0	0	5	8	10	6	8	8	3	7	6	3	5	4	4	0	2	1	.	.	.	.	.	.	.	.	.	.	
18	F	P	3	0	0	0	0	0	0	6	8	5	9	8	7	3	5	8	1	6	2	3	1	0	0	1	1	.	.	.	.	.	.	.	
19	F	1	3	0	0	0	0	0	5	7	6	7	7	5	6	5	7	5	6	7	5	5	3	3	2	0	1	1	.	.	.	.	.	.	
20	F	2	3	0	0	0	0	0	4	8	5	7	10	5	6	8	7	6	6	6	3	4	6	1	1	1	0	1	.	.	.	.	.	.	
21	G	P	3	0	0	0	0	0	0	7	9	9	6	8	7	7	10	8	5	6	2	5	2	2	1	1	1	.	.	.	.	.	.	.	
22	G	1	3	0	0	0	0	0	4	8	5	9	9	4	7	4	2	6	5	6	5	2	2	1	1	1	0	1	.	.	.	.	.	.	
23	G	2	3	0	0	0	0	0	4	5	7	8	5	6	8	6	6	4	4	1	4	2	3	2	1	1	.	.	.	.	.	.	.	.	
24	G	3	3	0	0	0	0	0	7	7	9	8	6	6	6	8	4	3	6	4	5	3	1	2	2	1	.	.	.	.	.	.	.	.	
25	H	P	3	0	0	0	0	0	0	4	7	7	6	7	8	5	6	4	5	7	4	5	6	3	4	1	.	.	.	.	.	.	.	.	

TABLE I (Continued)

				Daily Offspring Count																																
				Days																																
0	L	T	R	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	
26	H	1	3	0	0	0	0	0	0	8	7	8	4	8	6	6	4	8	7	3	7	4	5	3	5	4	2	1	1	.	.	.	.	.	.	
27	H	2	3	0	0	0	0	0	5	7	9	7	6	8	6	4	7	5	6	7	5	6	0	2	.	.	.	.	.	.	.	.	.	.	.	
28	H	3	3	0	0	0	0	0	3	9	5	8	6	4	5	4	4	6	3	3	4	3	3	3	3	2	.	.	.	.	.	.	.	.	.	
29	I	P	3	0	0	0	0	0	0	5	9	6	7	4	7	6	7	8	7	2	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	
30	I	1	3	0	0	0	0	0	0	3	8	2	9	6	7	4	5	5	2	4	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	
31	I	2	3	0	0	0	0	0	2	5	8	4	7	4	5	6	6	8	4	4	3	4	3	2	5	3	3	2	0	2	.	.	.	.	.	
32	I	3	3	0	0	0	0	0	0	7	8	9	8	8	7	8	5	8	5	3	4	4	2	0	1	1	0	2	.	.	.	.	.	.	.	
33	J	P	3	0	0	0	0	0	0	2	5	7	4	6	6	2	7	5	5	4	3	1	2	1	.	.	.	.	.	.	.	.	.	.	.	
34	J	1	3	0	0	0	0	0	0	6	8	5	9	6	5	6	5	5	7	8	6	6	9	2	6	3	3	2	.	.	.	.	.	.	.	
35	J	2	3	0	0	0	0	0	2	5	6	7	8	7	6	8	5	4	6	3	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	
36	J	3	3	0	0	0	0	0	0	0	3	5	5	8	7	6	8	7	7	5	5	5	5	2	2	.	.	.	.	.	.	.	.	.		
37	A	P	1	0	0	0	0	0	5	5	5	8	5	7	5	4	6	5	3	6	3	3	4	1	2	0	1	1	0	1	.	.	.	.	.	
38	A	P	2	0	0	0	0	0	0	1	6	6	10	9	5	5	8	4	7	4	3	0	1	.	.	.	.	.	.	.	.	.	.	.	.	
39	A	1	1	0	0	0	0	0	0	1	6	6	10	9	5	5	8	4	7	4	3	0	1	.	.	.	.	.	.	.	.	.	.	.	.	
40	A	1	2	0	0	0	0	0	0	2	5	5	3	4	5	5	6	5	6	5	5	9	5	3	6	1	3	2	1	.	.	.	.	.	.	
41	A	2	2	0	0	0	0	0	0	3	2	4	5	5	9	6	5	2	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
42	A	3	1	0	0	0	0	0	0	0	0	0	0	0	4	4	6	8	5	6	5	7	9	4	7	8	6	3	3	2	1	.	.	.	.	
43	A	3	2	0	0	0	0	0	0	7	8	10	11	6	8	5	7	7	6	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
44	B	P	1	0	0	0	0	0	0	8	6	6	4	7	3	6	5	3	5	4	4	2	2	2	1	.	.	.	.	.	.	.	.	.	.	
45	B	1	1	0	0	0	0	0	0	7	7	9	5	6	5	4	7	4	3	4	5	4	3	1	.	.	.	.	.	.	.	.	.	.	.	
46	B	2	1	0	0	0	0	0	2	6	9	8	9	7	6	9	6	6	4	5	1	4	2	2	1	1	.	.	.	.	.	.	.	.	.	
47	B	3	1	0	0	0	0	0	0	0	0	2	3	4	5	6	5	7	7	4	6	5	3	1	.	.	.	.	.	.	.	.	.	.		
48	C	P	1	0	0	0	0	0	0	5	8	5	10	7	8	6	6	7	6	5	6	2	4	4	0	1	.	.	.	.	.	.	.	.	.	
49	C	2	1	0	0	0	0	0	0	4	6	8	6	9	6	7	7	7	4	5	5	3	4	1	.	.	.	.	.	.	.	.	.	.		
50	C	3	1	0	0	0	0	0	0	4	5	5	8	5	6	6	6	7	7	7	5	6	5	3	3	4	4	1	1	.	.	.	.	.		
51	D	P	1	0	0	0	0	0	0	5	7	5	5	6	6	3	6	5	4	4	5	2	4	4	0	4	0	0	2	0	0	0	1	0	1	
52	D	1	1	0	0	0	0	0	0	4	9	6	7	8	8	4	8	6	6	6	4	3	4	1	1	1	.	.	.	.	.	.	.	.	.	
53	D	2	1	0	0	0	0	0	0	5	6	6	6	6	6	4	8	6	4	7	3	4	3	4	3	1	1	.	.	.	.	.	.	.	.	
54	D	3	1	0	0	0	0	0	0	4	4	4	4	4	2	6	4	5	2	4	6	5	0	0	0	0	1	1	0	0	1	.	.	.	.	
55	E	P	1	0	0	0	0	0	2	6	7	9	4	8	8	7	10	5	7	5	3	2	3	3	1	.	.	.	.	.	.	.	.	.		
56	E	1	1	0	0	0	0	0	0	3	7	8	5	6	7	6	5	6	8	7	6	2	7	2	3	3	3	1	1	.	.	.	.	.	.	

TABLE I (Continued)

O	L	T	R	Daily Offspring Count																															
				Days																															
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
57	E	2	1	0	0	0	0	0	0	0	4	6	8	4	9	7	6	8	9	8	4	6	5	4	2	2	1	1	.	.	.	.	.	.	.
58	E	3	1	0	0	0	0	0	4	4	7	7	5	9	8	7	7	3	5	4	2	1	1	1	.	.	.	.	.	.	.	.	.	.	.
59	F	P	1	0	0	0	0	0	0	4	6	9	7	8	7	5	7	5	10	6	6	6	5	2	1	.	.	.	.	.	.	.	.	.	.
60	F	1	1	0	0	0	0	0	0	0	8	7	7	5	7	4	8	6	8	5	5	3	.	.	.	.	.	.	.	.	.	.	.	.	.
61	F	2	1	0	0	0	0	0	0	5	8	5	7	7	6	4	4	6	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
62	F	3	1	0	0	0	0	0	0	6	8	8	7	8	8	5	7	5	5	5	3	5	3	3	2	2	1	.	.	.	.	.	.	.	
63	G	P	1	0	0	0	0	0	0	4	7	5	7	6	6	7	6	5	4	4	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.
64	G	1	1	0	0	0	0	0	0	8	6	5	5	3	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
65	G	2	1	0	0	0	0	0	0	4	6	8	8	8	9	8	8	6	7	3	2	1	.	.	.	.	.	.	.	.	.	.	.	.	
66	H	P	1	0	0	0	0	0	0	6	6	5	6	5	5	3	6	2	0	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	
67	H	1	1	0	0	0	0	0	0	3	7	6	6	8	5	8	7	8	6	4	4	1	2	.	.	.	.	.	.	.	.	.	.	.	
68	H	2	1	0	0	0	0	0	0	8	6	7	4	6	8	4	5	6	5	5	5	6	4	5	1	2	1	.	.	.	.	.	.	.	
69	I	P	1	0	0	0	0	0	0	4	5	6	5	6	4	4	5	5	4	3	.	6	5	4	4	4	0	1	.	.	.	.	.	.	.
70	I	1	1	0	0	0	0	0	0	6	6	6	7	8	8	7	8	7	4	5	2	5	0	4	0	2	.	.	.	.	.	.	.	.	
71	I	2	1	0	0	0	0	0	0	0	0	3	2	1	5	2	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
72	I	3	1	0	0	0	0	0	0	6	8	8	8	1	0	8	5	7	6	7	7	4	3	6	3	1	1	.	.	.	.	.	.	.	
73	J	P	1	0	0	0	0	0	0	4	6	6	8	4	5	9	5	8	7	5	5	4	4	3	2	1	3	3	.	.	.	.	.	.	.
74	J	1	1	0	0	0	0	0	0	1	7	6	5	6	7	5	7	3	6	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.
75	J	2	1	0	0	0	0	0	1	5	8	4	8	8	5	6	9	6	6	3	3	4	6	4	3	4	2	.	.	.	.	.	.	.	
76	J	3	1	0	0	0	0	0	0	5	9	8	5	7	6	6	1	1	5	5	5	2	4	2	1	.	.	.	.	.	.	.	.	.	
77	A	P	4	0	0	0	0	0	0	3	5	6	9	6	7	4	5	7	3	5	5	4	5	3	4	4	2	3	2	1	.	.	.	.	
78	A	1	4	0	0	0	0	0	0	0	2	4	5	6	5	5	7	4	6	4	4	4	5	4	4	2	1	.	.	.	.	.	.	.	
79	A	2	4	0	0	0	0	0	2	8	7	7	7	8	6	8	7	10	8	5	5	5	3	3	3	2	1	.	.	.	.	.	.	.	
80	A	3	4	0	0	0	0	0	2	6	8	7	7	8	6	7	7	3	.	5	1	2	1	0	11	1	11	0	1	.	.	.	.	.	
81	C	P	4	0	0	0	0	0	0	3	4	7	9	5	6	5	7	2	2	5	1	1	1	2	2	1	2	0	0	3	2	4	0	2	2
82	C	1	4	0	0	0	0	0	0	4	7	6	8	6	7	6	7	5	6	5	5	4	4	4	3	3	1	1	1	.	.	.	.	.	
83	C	2	4	0	0	0	0	0	0	4	6	6	8	5	6	6	5	6	7	6	6	4	3	1	1	3	1	.	.	.	.	.	.	.	
84	C	3	4	0	0	0	0	0	0	1	3	5	5	5	7	7	8	5	4	4	3	4	2	1	1	1	.	.	.	.	.	.	.	.	
85	D	P	4	0	0	0	0	0	1	5	3	5	4	6	5	4	5	4	5	4	6	7	3	5	5	3	6	4	2	4	2	.	.	.	
86	D	1	4	0	0	0	0	0	0	4	4	6	6	5	3	5	3	6	5	7	7	7	4	6	6	5	4	4	3	.	.	.	.	.	
87	D	2	4	0	0	0	0	0	0	4	6	7	6	6	6	5	6	6	7	6	6	3	3	6	3	3	3	1	.	.	.	.	.	.	

TABLE I (Continued)

O	L	T	R	Daily Offspring Count																															
				Days																															
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
88	D	3	4	0	0	0	0	0	0	5	9	8	8	10	10	10	9	4	6	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
89	E	P	4	0	0	0	0	0	0	2	6	6	9	7	8	7	8	8	8	4	5	4	3	4	4	0	1	.	.	.	.	.	.	.	
90	E	1	4	0	0	0	0	0	0	0	8	6	5	9	6	5	4	5	4	5	5	5	4	4	3	6	0	2	1	1	1	.	.	.	
91	E	2	4	0	0	0	0	0	0	8	6	10	9	8	8	7	6	7	7	6	4	2	3	2	2	.	.	.	.	.	.	.	.	.	
92	E	3	4	0	0	0	0	0	0	4	9	6	8	8	8	9	9	8	7	6	6	4	2	0	1	.	.	.	.	.	.	.	.	.	
93	F	P	4	0	0	0	0	0	0	3	3	4	4	5	5	5	3	2	5	5	3	2	5	4	4	4	4	3	4	2	1	1	.	.	
94	F	1	4	0	0	0	0	0	0	2	7	7	8	6	6	7	5	6	6	4	5	4	7	5	3	2	.	.	.	.	.	.	.	.	
95	F	2	4	0	0	0	0	0	0	1	3	4	5	6	5	4	6	4	6	3	7	3	9	1	5	3	4	5	.	.	.	.	.	.	
96	F	3	4	0	0	0	0	0	0	7	7	9	7	8	9	9	6	8	5	4	4	4	5	1	2	1	.	.	.	.	.	.	.	.	
97	G	P	4	0	0	0	0	0	0	3	8	8	7	8	3	6	6	5	7	7	5	7	4	4	2	1	1	1	.	.	.	.	.	.	
98	G	1	4	0	0	0	0	0	0	5	7	6	8	7	4	7	2	8	7	5	9	3	8	2	7	5	0	3	2	0	1	.	.	.	
99	G	2	4	0	0	0	0	0	0	4	4	6	8	7	5	6	7	8	6	3	4	5	8	.	.	.	.	.	.	.	.	.	.	.	
100	G	3	4	0	0	0	0	0	1	7	5	4	9	5	6	6	6	3	7	5	4	5	3	7	5	1	1	1	.	.	.	.	.	.	
101	H	P	4	0	0	0	0	0	0	1	7	6	6	7	8	4	6	5	5	4	7	5	3	5	1	2	3	0	2	1	1	1	1	0	1
102	H	1	4	0	0	0	0	0	0	4	5	5	5	6	5	6	5	6	6	5	4	3	7	3	6	3	5	3	1	1	0	1	.	.	
103	H	2	4	0	0	0	0	0	0	2	6	6	5	6	8	5	7	6	6	7	6	3	6	7	3	1	1	1	.	.	.	.	.	.	
104	I	P	4	0	0	0	0	0	3	6	8	8	7	7	10	8	7	4	4	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
105	I	1	4	0	0	0	0	0	0	5	8	5	8	8	7	7	6	4	7	6	5	5	4	2	0	1	.	.	.	.	.	.	.	.	
106	I	2	4	0	0	0	0	0	0	10	6	5	5	7	2	8	5	5	9	7	8	3	5	2	1	2	1	.	.	.	.	.	.	.	
107	J	P	4	0	0	0	0	0	0	4	7	4	6	5	5	4	6	7	5	6	6	4	5	4	6	2	1	1	1	.	.	.	.	.	
108	J	1	4	0	0	0	0	0	0	7	6	6	9	4	9	6	5	5	7	5	5	4	2	3	0	1	.	.	.	.	.	.	.	.	
109	J	2	4	0	0	0	0	0	0	4	6	5	10	5	7	7	5	7	6	9	6	4	2	1	1	1	.	.	.	.	.	.	.	.	
110	J	3	4	0	0	0	0	0	2	7	9	8	9	9	8	10	9	7	7	4	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.

<sup>a</sup> Observations<sup>b</sup> Locations are: A = Kingfisher; B = Wichita; C = Hobart; D = Sparks; E = Chickasha; F = Rossevelt;  
G = Stillwater; H = Perkins; I = Yale; J = Ponca City<sup>c</sup> Types are: P = parent; 1 = first offspring; 2 = offspring one week after larviposition; 3 = offspring  
two weeks after larviposition.<sup>d</sup> Replications



TABLE II

VALUES OF REPRODUCTIVE VARIABLES, BY TYPE AND LOCATION, OF A  
 PARTHENOGENETICALLY REPRODUCING SCHIZAPHIS GRAMINUM  
 (RONDANI). STILLWATER, OK, SUMMER 1982

O <sup>a</sup>	L <sup>b</sup>	T <sup>c</sup>	R <sup>d</sup>	Values of Reproductive Variables					
				Reproductive Variables <sup>e</sup>					
				PP	OPRO	FECU	RP	LONG	PORP
1	A	P	3	6	4.5	45	10	18	2
2	A	1	3	5	3.8	100	26	36	5
3	A	2	3	6	3.1	71	23	42	13
4	B	P	3	6	2.0	8	4	22	12
5	B	1	3	6	4.3	90	21	28	1
6	C	P	3	5	5.6	89	16	40	19
7	C	1	3	6	5.3	64	12	18	0
8	C	2	3	5	4.1	83	20	42	17
9	C	3	3	5	5.6	78	14	46	27
10	D	P	3	5	5.6	96	17	44	22
11	D	1	3	6	5.3	107	20	48	22
12	D	2	3	5	5.8	98	17	38	16
13	D	3	3	6	4.0	104	26	40	8
14	E	P	3	5	4.1	94	23	43	15
15	E	1	3	6	4.8	96	20	45	19
16	E	2	3	5	5.0	85	17	38	16
17	E	3	3	5	5.0	80	16	40	19
18	F	P	3	6	4.1	74	18	24	0
19	F	1	3	5	4.6	93	20	42	17
20	F	2	3	5	4.8	95	20	41	16
21	G	P	3	6	5.3	96	18	41	17
22	G	1	3	5	4.1	83	20	39	14
23	G	2	3	5	4.3	77	18	44	21
24	G	3	3	5	4.9	88	18	45	22
25	H	P	3	6	5.2	89	17	37	14
26	H	1	3	6	5.0	101	20	44	18
27	H	2	3	5	5.6	90	16	40	19
28	H	3	3	5	4.3	78	18	47	24
29	I	P	3	6	5.1	71	14	42	22
30	I	1	3	6	4.2	59	14	31	11
31	I	2	3	5	4.1	90	22	.	.
32	I	3	3	6	4.7	90	19	45	20
33	J	P	3	6	4.0	60	15	25	4
34	J	1	3	6	5.7	109	19	48	23
35	J	2	3	5	4.8	72	15	40	20
36	J	3	3	7	5.3	80	15	32	10
37	A	P	1	5	3.6	80	22	43	16
38	A	P	2	6	4.9	69	14	44	24
39	A	1	1	6	4.9	69	14	44	24
40	A	1	2	6	4.3	86	20	41	15
41	A	2	2	6	3.6	43	12	.	.
42	A	3	1	11	5.2	88	17	52	24

TABLE II (Continued)

O	L	T	R	Values of Reproductive Variables					
				Reproductive Variables					
				PP	OPRO	FECU	RP	LONG	PORP
43	A	3	2	6	6.7	80	12	43	25
44	B	P	1	6	4.3	68	16	22	0
45	B	1	1	6	4.9	74	15	31	10
46	B	2	1	5	4.9	88	18	41	18
47	B	3	1	8	4.5	58	13	35	14
48	C	P	1	6	5.3	90	17	45	22
49	C	2	1	6	5.5	82	15	45	24
50	C	3	1	6	4.9	98	20	46	20
51	D	P	1	6	3.0	79	26	32	0
52	D	1	1	6	5.1	86	17	37	14
53	D	2	1	6	4.6	83	18	33	9
54	D	3	1	7	2.5	53	21	28	0
55	E	P	1	5	5.3	90	17	26	4
56	E	1	1	6	4.8	96	20	45	19
57	E	2	1	7	5.2	94	18	45	20
58	E	3	1	5	4.7	75	16	43	22
59	F	P	1	6	5.9	94	16	43	21
60	F	1	1	7	6.1	73	12	25	6
61	F	2	1	6	5.5	55	10	.	.
62	F	3	1	6	5.1	91	18	47	23
63	G	P	1	6	4.7	66	14	42	22
64	G	1	1	6	4.6	32	7	.	.
65	G	2	1	6	6.0	78	13	44	25
66	H	P	1	6	3.7	48	13	20	1
67	H	1	1	6	5.4	75	14	42	22
68	H	2	1	6	4.9	88	18	44	20
69	I	P	1	6	4.2	79	19	46	21
70	I	1	1	6	5.0	85	17	44	21
71	I	2	1	8	2.3	18	8	18	2
72	I	3	1	6	5.7	91	16	39	17
73	J	P	1	6	4.8	87	18	48	24
74	J	1	1	6	4.7	56	12	.	.
75	J	2	1	5	4.8	92	19	45	21
76	J	3	1	6	5.4	76	14	42	22
77	A	P	4	6	4.4	88	20	46	20
78	A	1	4	7	4.3	68	16	48	25
79	A	2	4	5	5.6	100	18	41	18
80	A	3	4	5	3.7	78	21	43	17
81	C	P	4	6	2.9	79	27	37	4
82	C	1	4	7	4.7	89	19	48	22
83	C	2	4	6	4.9	83	17	50	27
84	C	3	4	6	4.1	65	16	44	22
85	D	P	4	5	4.2	93	22	49	22
86	D	1	4	7	4.9	99	20	46	19

TABLE II (Continued)

O	L	T	R	Values of Reproductive Variables					
				Reproductive Variables					
				PP	OPRO	FECU	RP	LONG	PORP
87	D	2	4	6	4.9	93	19	46	21
88	D	3	4	6	7.1	92	13	43	24
89	E	P	4	6	5.2	94	18	47	23
90	E	1	4	7	4.2	89	21	48	20
91	E	2	4	6	5.9	95	16	46	24
92	E	3	4	6	5.9	95	16	42	20
93	F	P	4	6	3.5	81	23	48	19
94	F	1	4	6	5.3	90	17	47	24
95	F	2	4	6	4.4	84	19	44	19
96	F	3	4	6	5.6	96	17	42	19
97	C	P	4	6	4.9	93	19	48	23
98	G	1	4	6	4.8	106	22	44	16
99	G	2	4	6	5.8	81	14	39	19
100	G	3	4	5	4.5	91	20	46	21
101	H	P	4	6	3.5	92	26	45	13
102	H	1	4	7	4.1	95	23	43	13
103	H	2	4	6	4.8	92	19	50	25
104	I	P	4	5	5.8	76	13	38	20
105	I	1	4	7	5.2	88	17	67	23
106	I	2	4	6	5.1	91	18	47	23
107	J	P	4	6	4.4	89	20	46	20
108	J	1	4	6	4.9	84	17	44	21
109	J	2	4	6	5.1	86	17	45	22
110	J	3	4	5	6.9	96	14	41	22

<sup>a</sup>Observations<sup>b</sup>Locations are: A = Kingfisher; B = Wichita; C = Hobart; D = Sparks;  
E = Chickasha; F = Roosevelt; G = Stillwater; H = Perkins;  
I = Yale; J = Ponca City.<sup>c</sup>Types are: P = parent; 1 = first offspring; 2 = offspring one week after  
larviposition; 3 = offspring two weeks after larviposition.<sup>d</sup>Replications<sup>e</sup>Reproductive variables are: PP = prereproductive period; RP = reproductive  
period; PORP = postreproductive period; LONG =  
longevity; FECU = fecundity; OPRP = offspring  
per day of reproductive period.

A = 14      G = 10  
 B = 6      I = 11  
 C = 12      J = 12  
 D = 12  
 E = 12      100  
 F = 11

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VITA

Million Abebe

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